

THE SYSTEMATIC VALUE OF TRICHOME
COMPLEMENTS IN A NORTH AMERICAN GROUP
OF VERNONIA (COMPOSITAE)

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Trichomes are among the most useful of all anatomical features for systematic comparisons of angiosperms. This is because of their variety, their wide occurrence, their ease of preparation for study, and sometimes their close correlations to variation patterns among the taxa (Carlquist, 1961). The characteristic forms of trichomes are often of considerable value in recognition of genera (Heintzelman & Howard, 1948), and certain distinct types of trichomes may be used as criteria for distinguishing species (Cowan, 1950; Goodspeed, 1954). In *Nicotiana*, Goodspeed (1954) found that the trichome complement is of phyletic significance because the types of trichomes point to species origins and relationships. The trichome complements in *Nicotiana* are correlated with patterns of morphology, geographical distribution, and cytogenetics. Cowan (1950) demonstrated that trichomes are a reliable guide to relationships and classification in *Rhododendron*.

Uniseriate trichomes as well as a variety of multicellular glandular and non-glandular trichomes are widely distributed in *Vernonia* (Solereeder, 1908). Hunter and Austin (1967) demonstrated the hybrid origin of a *Vernonia* taxon by a comparison of the trichome complement of the two parental species and their hybrid progeny. They suggested that a study of the trichomes of other species of *Vernonia* might be of taxonomic significance. Urbatsch (1972), Faust (1972), and King (1971), working on systematic problems among the species of *Vernonia* native to the United States, found evidence that trichomes are of systematic value in the genus. In 1923, Gleason erected a series of hypotheses on migration and evolution of *Vernonia* in North America. These hypotheses provide a basis of comparison for studies of trichome patterns and schemes

of phyletic groupings. More recently, *Vernonia* has been the subject of a series of biosystematic and biochemical investigations by Jones and his students and by Abdel-Baset and Padolina in Dr. Tom Mabry's laboratory at the University of Texas. These later studies have provided additional data and an opportunity to refine Gleason's hypotheses.

Living material of 21 taxa of a closely related group of *Vernonia*, the *Paniculatae verae*, from the Sierra Madre Oriental of Mexico and from the eastern one-half of the United States were available in the greenhouse. This provided an opportunity to determine whether or not trichome complements might provide information useful in the classification of these *Vernonia* species. This evidence along with other data from biochemical systematics, transplant studies, hybridization experiments, and population analyses will eventually be combined into a taxonomic revision of the subsection *Paniculatae verae*.

MATERIALS AND METHODS

Mid-cauline leaves of each taxon collected from greenhouse grown transplants were fixed in FPA (formaldehyde, propionic acid, and alcohol) for anatomical comparisons. Whole mounts of leaves were cleared in 1% aqueous NaOH at 60°C and transferred to 75% lactic acid at 60°C until completely cleared. The leaves were then stained in safranin and fast green and mounted in Hoyer's solution. Leaves from herbarium specimens were cleared in the same manner for additional observations. Leaf cross-sections were prepared by dehydrating in an ethyl alcohol-butanol series, embedding in paraffin, and sectioning at 12 μ . The sections were stained with safranin and fast green. Fresh whole mounts of the leaves, 3 mm², were examined by scanning electron microscopy. The whole mounts were glued onto the specimen stubs with a mixture of Elmer's Glue-All and silver conductive paint. Micrographs were made of the trichome types. Paired affinity indexes were constructed for the trichome complement of the lower leaf surfaces as

TABLE 1. Leaf trichome complements of 21 taxa of *Vernonia*.

Taxon ¹	Trichome type ²						
	Bilobed	Awl-shaped glandular	Awl-shaped glandular	L-shaped glandular	L-shaped glandular	T-shaped	Uniseriate Longhorn
<i>V. schaffneri</i>	B	B	L				U
<i>V. greggii</i>	B	L	L				U
<i>V. ervendbergii</i>	L	B					B
<i>V. texana</i>	B	U	L				B
<i>V. arkansana</i>	B	B	B				U
<i>V. angustifolia</i>	B	L	L				U
<i>V. pulchella</i>	L	B	B				B
<i>V. glauca</i>	B	L	L				U
<i>V. larsenii</i>	B		L				B
<i>V. lindheimeri</i>	B		L				B
<i>V. flaccidifolia</i>		L		L	B		U
<i>V. lettermannii</i>	B		L				
<i>V. noveboracensis</i>	B	L	L	B			U
<i>V. blodgettii</i>	B	U	L	L			
<i>V. acaulis</i>	L	L	L				B
<i>V. gigantea</i>	B	L	L				U
* <i>V. bald. ssp. bald.</i>	B	L	L		L	L	U
* <i>V. bald. ssp. int.</i>	B	L	L			L	B
<i>V. missurica</i>	B	U	B	L			U
<i>V. fasciculata</i>	B	L	L	U			U
<i>V. marginata</i>	B	L	L	U			U

¹The taxonomic treatment is based on that of Gleason, 1922, as modified by Jones, 1964, 1970; Urbatsch, 1972; Faust, 1972; King, 1971.

²Occurrence on leaves is indicated by abbreviations: U = upper surface only; L = lower surface only; B = present on both surfaces.

**V. bald. ssp. bald* = *V. baldwinii* ssp. *baldwinii*; *V. bald. ssp. int.* = *V. baldwinii* ssp. *interior*.

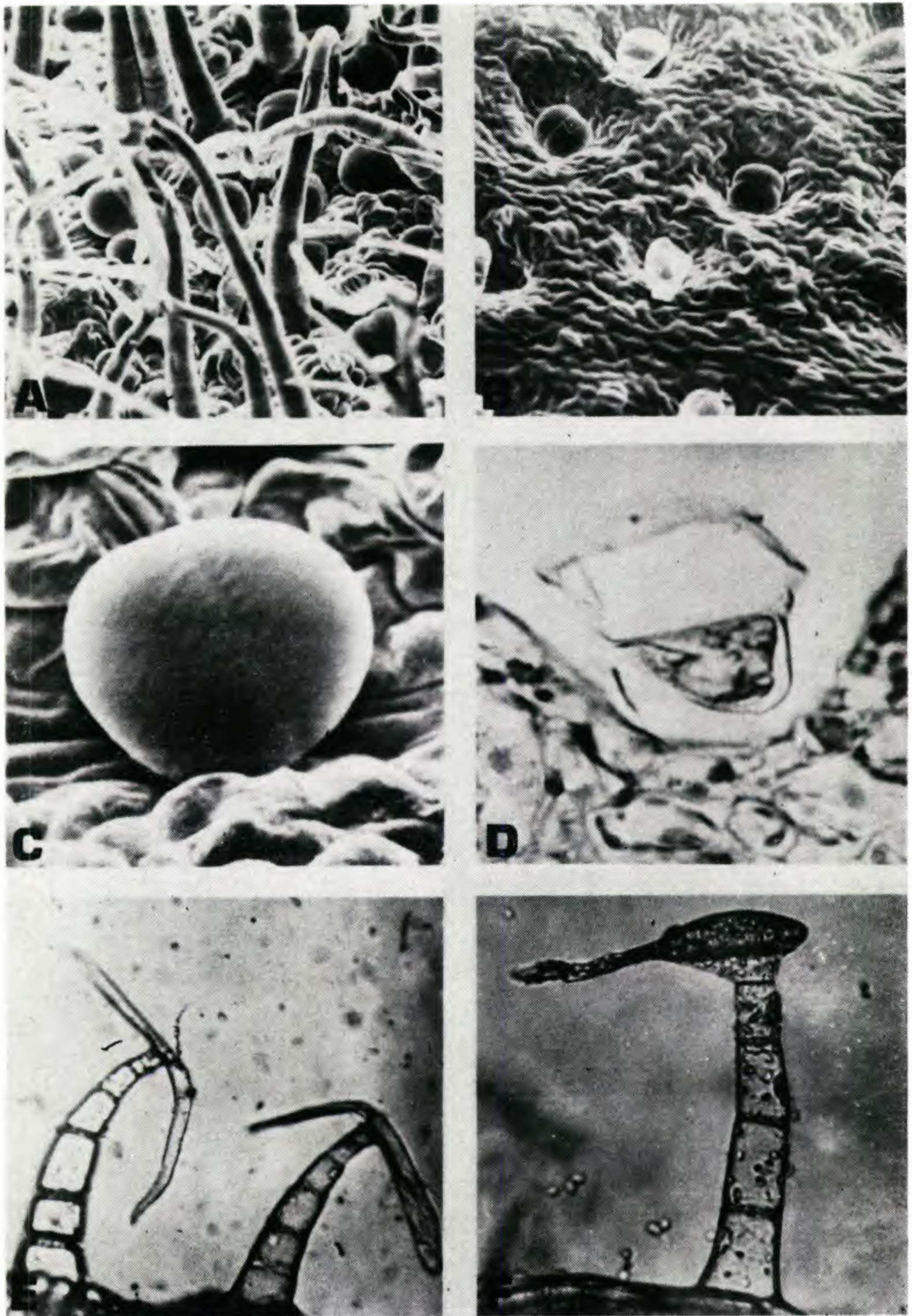


Figure 1. Trichomes on lower leaf surfaces of *Vernonia*: (A) SEM of *V. missurica* 100 \times , (B) SEM of *V. marginata* bilobed and awl-shaped types 100 \times , (C) SEM of *V. marginata* bilobed type 500 \times , (D) cross-section of *V. marginata* bilobed type illustrating basal cells 500 \times , (E) whole mount of *V. baldwinii* ssp. *interior* T-shaped type 400 \times , (F) whole mount of *V. baldwinii* ssp. *baldwinii* L-shaped glandular type 400 \times .

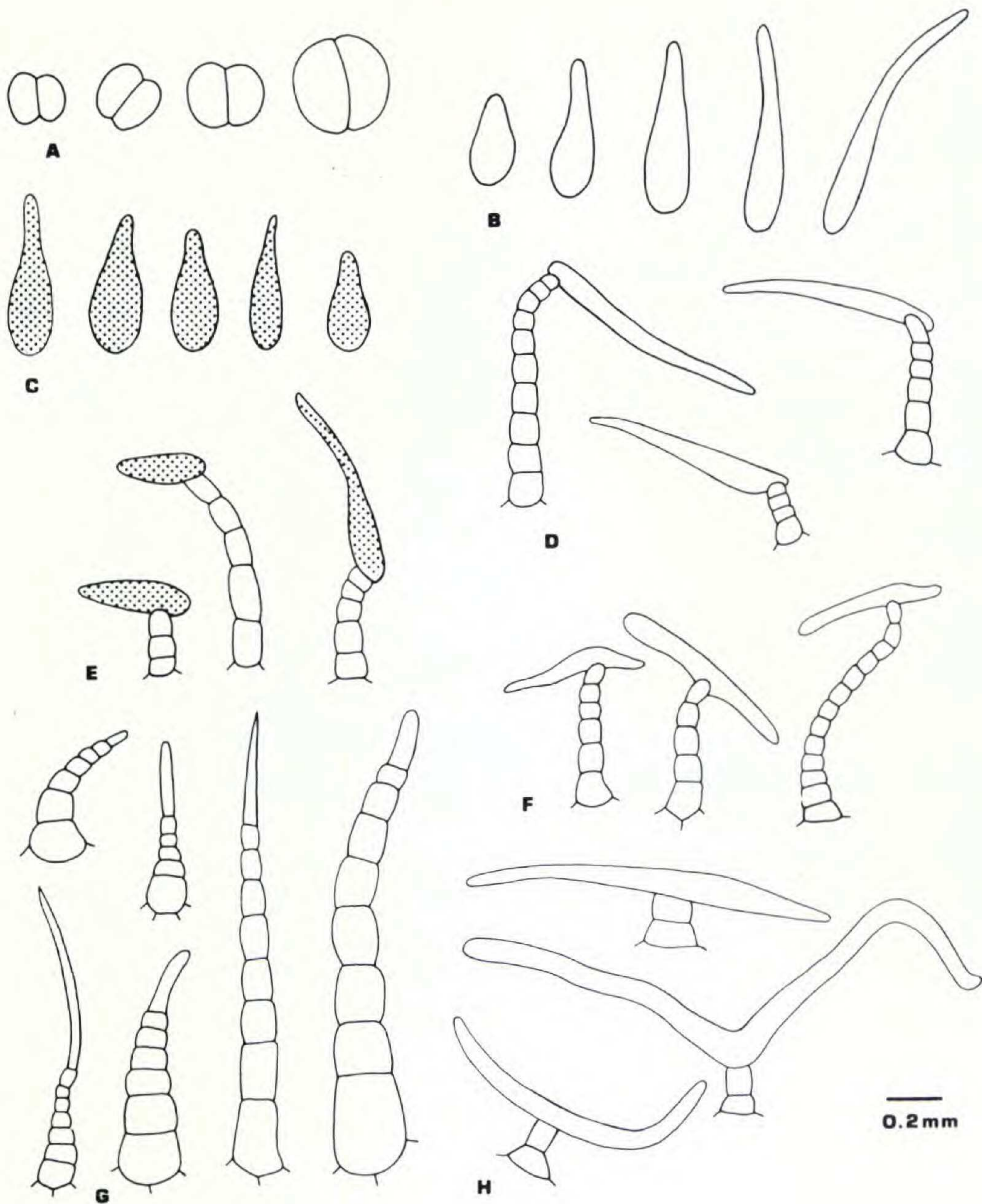


Figure 2. Line drawings of populations of the trichome types of *Vernonia*: (A) bilobed, (B) awl-shaped, (C) awl-shaped glandular, (D) L-shaped, (E) L-shaped glandular, (F) T-shaped, (G) uniseriate, (H) longhorn. Trichomes selected include typical and extreme forms.

they usually are the most reliable guide to relationships (Cowan, 1950):

$$\text{Paired affinity index} = \frac{\text{trichome types common to both species}}{\text{total trichome types of both species}} \times 100.$$

RESULTS AND DISCUSSION

The trichome complements of 21 taxa of *Vernonia* are presented in Table 1 along with their distributions on the leaves. Photomicrographs and scanning electron micrographs of selected trichomes are shown in Figure 1. Populations of the trichome types are illustrated by camera lucida drawings in Figure 2. Comparison of possible arrangements of the taxa, based upon trichome complements with those groupings suggested by Gleason (1906, 1922, 1923) indicated that trichomes in *Vernonia* may indeed have some phyletic significance. Analysis of the trichome complement on both the upper and lower leaf surfaces suggested that certain species or groups of species stand apart from the other species (see Table 1). For example, *V. larsenii* and *V. lindheimeri* are closely related based upon gross morphology as well as upon trichome complement (King, 1971). They are the only taxa with the longhorn trichome type. *Vernonia larsenii* and *V. lindheimeri* also possess the same 15 flavonoid compounds and the same major sesquiterpene lactone, Glaucolide-F (Abdel-Baset and Padolina, per. com.). *Vernonia flaccidifolia* is the only species which does not have the bilobed trichome type. The taxon contains only one flavonoid compound and no sesquiterpene lactones (Abdel-Baset and Padolina, per. com.). Therefore, as Gleason (1923) suggested, *V. flaccidifolia* may be more advanced and evolutionarily specialized than some of the other species of *Vernonia*. *Vernonia fasciculata* and *V. marginata*, placed in the Fasciculatae group by Gleason (1923), possess the same types of trichomes on both the upper and lower surfaces of leaves (Jones, 1972). Chemical evidence indicates a close relationship; *V. marginata* and *V. fasciculata* have identical flavonoid com-

pounds (Abdel-Baset and Padolina, per. com.). Also, these two species along with *V. arkansana* contain Glaucolide-M as the major sesquiterpene lactone compound.

Examination of the paired affinity indexes of the trichome complement of the lower leaf surfaces (Table 2) indicate several natural groupings. *Vernonia schaffneri*, *V. greggii*, *V. arkansana*, *V. angustifolia*, *V. fasciculata*, and *V. marginata* each have a paired affinity index of 100 to each other. Two of these species, *V. schaffneri* and *V. greggii* of Mexico, were considered by Gleason (1923) to be from the most primitive stock based upon morphology and phytogeography. *Vernonia schaffneri*, *V. greggii*, *V. ervendbergii*, and *V. texana* contain the same major sesquiterpene lactone, Glaucolide-A, and many identical flavonoid compounds (Abdel-Baset and Padolina, per. com.). *Vernonia gigantea* and *V. noveboracensis* have a paired affinity index of 100. They also possess the same flavonoid compounds and the same major sesquiterpene lactone compound, Glaucolide-A (Abdel-Baset and Padolina, per. com.). Gleason suggested that these two taxa evolved from the same ancestral line. The two species are similar in vegetative features such as leaf size and shape and stem height. *Vernonia noveboracensis* is a plant of wet soil, whereas *V. gigantea* grows in well drained soil. There are also differences in the number of flowers per head and in the length of the bract tips. On the other hand, it is difficult to distinguish vegetatively *V. gigantea* and *V. noveboracensis* grown in the greenhouse or the transplant garden unless the flowers are present.

Gleason (1923) proposed that the ancestral home of the genus *Vernonia*, as far as North American species are concerned, is tropical South America. He suggested that migration occurred from tropical South America through Central America and Mexico into Texas. From Texas migration accompanied by evolution proceeded in two directions, northward through the prairie region and eastward along the coastal plain. Speculation concerning the evolution of the taxa utilizing morphological and ecological

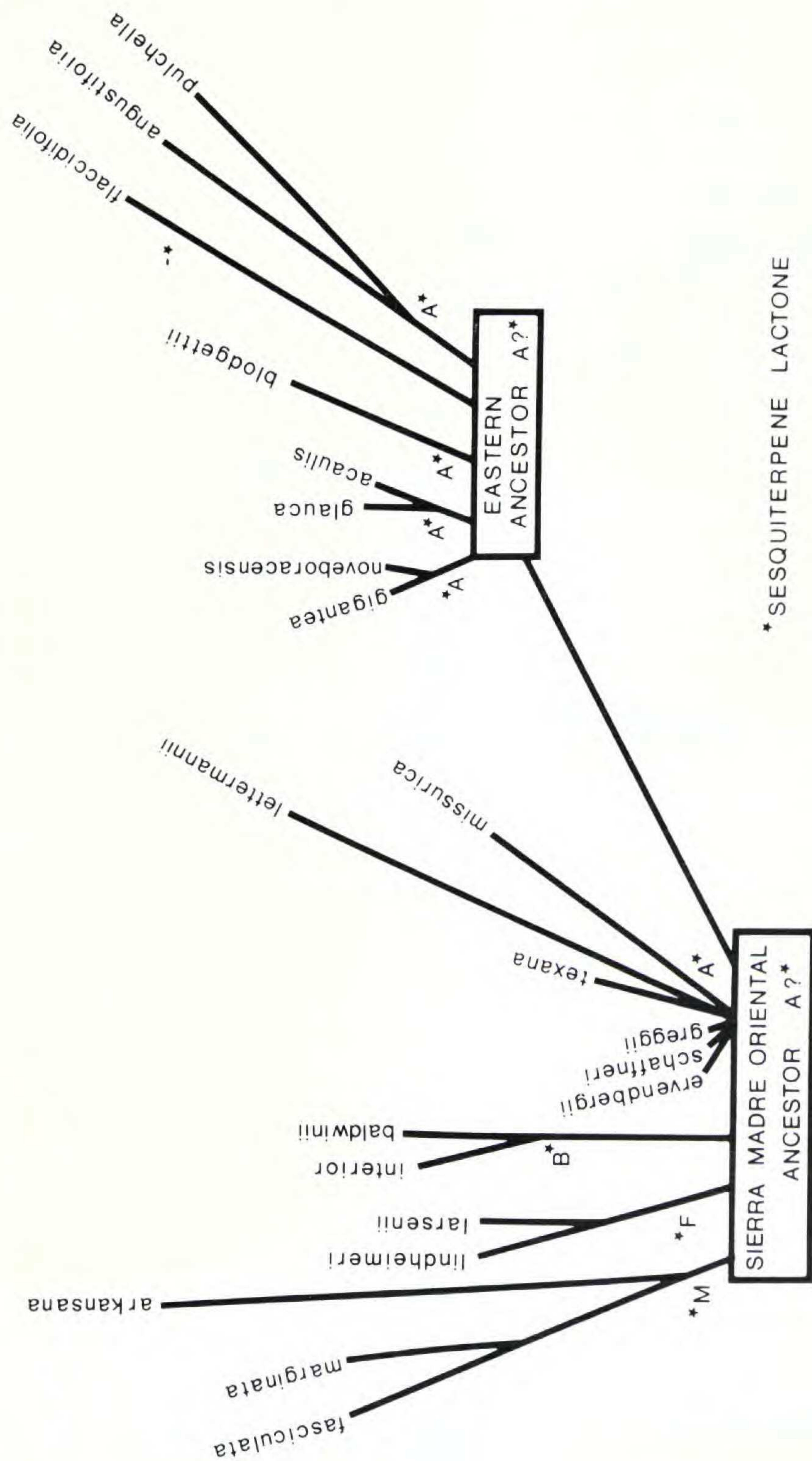


Figure 3. Diagrammatic scheme of migration and evolution of 21 taxa of *Vernonia*. Lines show distribution of the taxa by their location.

information and chemical data (Abdel-Baset and Padolina, per. com.) is presented in Figure 3. The western species of *Vernonia* have more flavonoids than do the eastern species of *Vernonia*. Generally, the western taxa contain from three to five compounds that are lacking in the eastern taxa. The eastern species have the same major sesquiterpene lactone, Glaucolide-A, that occurs in the species of *Vernonia* from the Sierra Madre Oriental of Mexico.

The use of the trichome complement as an aid to establishing relationships in *Vernonia* does have its limitations. For example, *V. blodgettii* and *V. missurica* have a paired affinity index of 100. Yet based upon morphological characters and geographic criteria they are very different. *Vernonia blodgettii* is a low, sparsely pubescent plant endemic to southern Florida, whereas *V. missurica* is a tall, extremely pubescent, wide-ranging species of the Mississippi Valley region. Another problem is presented by *V. baldwinii* ssp. *baldwinii* and ssp. *interior*. Evidence from morphological studies suggests close relationships (Faust, 1972). Populations of *V. baldwinii* ssp. *baldwinii* are found throughout the Ozark Plateaus province and the Ouachita province. *Vernonia baldwinii* ssp. *interior* populations occur primarily on the prairies and pastures of the central plains. The ranges of these two taxa overlap along the edges of the Ozarks and Ouachitas and a broad transition zone, or zone of intergradation is present (Faust, 1972). The characteristics of the intergradation zone surrounding the Interior Highlands suggest that the genomes of *V. baldwinii* ssp. *baldwinii* and ssp. *interior* are highly compatible and that the volume of gene flow between the two taxa may be relatively high. Additional evidence from biochemical systematics (Abdel-Baset and Padolina, per. com.) indicates a close relationship; the two subspecies contain the same major sesquiterpene lactone, Glaucolide-B. However, the trichome complement shows differences in the two subspecies. *Vernonia baldwinii* ssp. *baldwinii* has the L-shaped glandular trichome, whereas ssp. *interior* does not have this type. Also, uniseriate trichomes were

not found on the lower leaf surfaces of *V. baldwinii* ssp. *baldwinii*.

The evidence from this study suggests that trichomes can be diagnostic characteristics in *Vernonia*. However, their value as taxonomic criteria will be greatly increased if the information can be interpreted with reference to other lines of evidence such as that obtained from biochemical systematics, distributional studies, gross morphology, and hybridization experiments. All of the 21 taxa in this study form fully fertile F_1 hybrids but sometimes have hybrid breakdown in the F_2 and F_3 generations (Urbatsch, 1972; Faust, 1972; King, 1971; Jones, unpublished). Thus, trichome complement differentiation in this group of closely related plants must in some way be related to natural selection and the habitat that they occupy.

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